the Silurian seas. Moreover the family *Poritidæ*, which now includes many of the most important of reef-building corals, was also, even in palæozoic ages, a family rich in reef-forming species; for some of the species of *Favosites* grew into hemispherical masses eight or ten feet in diameter. It also seems probable that the genus *Alveopora* has existed through all periods from the palæozoic to the present time, which would seem the more remarkable considering the extreme delicacy and fragility of these corals, and also the fact that, so far as known, they are all shallow-water and reef species.

XXXVIII.—*On the Morphology and Affinities of Graptolites.* By Prof. Allman, F.R.S., F.L.S., &c.*

Among the extinct forms of life few possess more interest than these remarkable fossils, absolutely confined, as they are, to one great section of the palæozoic rocks, where their vast abundance, wide geographical distribution, and easy recognition render them of special value to the practical geologist.

The Graptolites are now by most palæontologists referred to the Hydroida: and their living representatives are sought for among the calyptoblastic genera of this order. While, however, I am unable to recognize their hydroid relations from the point of view from which palæontologists have generally agreed to regard them, I believe that their affinities with the Hydroida are too decided to justify their omission from any complete exposition of the palæontological history of this group of the animal kingdom.

The typical form of a graptolite is that of a narrow tube, straight or more or less curved, emitting from one side a series of hollow denticles, which are the free extremities of little cups or calicles, through which the cavity of the tube opens

* The following paper is mainly a portion of a chapter on the Distribution of the Hydroida in Time contained in the second part of the author's 'Monograph of the Gymnoblastic Hydroids' now nearly ready for delivery; and as it contains some new views of a question much agitated at this moment, it was thought that its regular publication might be here anticipated. The section of the work to which it properly belongs was printed off some time ago, and consequently before the appearance of Dr. Nicholson's 'Monograph of the British Graptolitidæ,' the first part of which, just published, will be welcomed by the palæontologist as a very valuable introduction to the systematic study of the graptolites. This difference of date will explain the absence of reference to Dr. Nicholson's work in the Monograph of the Gymnoblastea. Dr. Nicholson, however, does not seem to have essentially modified the views contained in his earlier publications and discussed in that Monograph.

externally, and having a solid slender rod ("virgula") imbedded in the walls of the opposite side. This type form ("monoprionidian") is represented by the genus *Graptolites* proper (fig. 1), where the calicles or tubular offsets from the common canal are in contact with one another at their bases and usually for a greater or less extent of their length, and by the genus *Rastrites*, where they are separated from one another by considerable intervals.

Fig. 1.

Longitudinal section of a fragment of *Graptolites priodon*, after Barrande.

But we may conceive of two such graptolites being united back to back; and the resulting form will then present two series of tubular offsets, one on one side of the main tube and the other on the side diametrically opposite, while the solid rod will now occupy the axis, holding just such a position as it would do if it had been formed by the union of the two rods of the component halves.

This form ("diprionidian") is represented by such genera as *Diplograptus*, where the tubular offsets stand out more or less free from the sides of the main tube, and by *Climacograptus*, where they are adnate to one another, so as to appear entirely immersed in its walls.

Some other forms also exist, such as *Dicranograptus*, in which the graptolite with a double row of denticles, after continuing its course for a time, divides into its component halves, which then diverge from the basal portion as two branches, constructed each on the single-rowed type. Branched single-rowed forms (*Cladograptus*, *Dichograptus*) also occur. In *Dichograptus* primary branches radiate from a common point at the proximal end, where they are connected by a web-like disk, apparently composed of a double membrane of the same nature as that which forms the walls of the branches*.

There are also some anomalous forms (*Retiolites*, *Phyllograptus*), whose structure has not yet been determined with sufficient certainty to admit of a satisfactory association with the true graptolites; but the essential features in the morphology of the graptolites, as well as their more important modifications, are expressed in the genera already cited.

There is sufficient evidence to show that the graptolites

* See Hall, 'Graptolites of the Quebec Group.'

were flexible, and that the solid parts, which are all that have come down to us, were of a horny or chitinous consistence. There is also evidence to show that, though some obscure forms (*Dendrograptus*), associated on insufficient grounds with the graptolites, were apparently rooted, the true graptolites were never directly attached to any other bodies—thus differing from the hydroid trophosomes and most of the corals and Polyzoa of the present day.

We are absolutely ignorant of the original contents of the main tube and of its lateral offsets, and we know just as little of other soft parts which may have accompanied the chitinous skeleton; so that in attempting to assign to the graptolites their position in the system of nature we are driven to analogy, by no means close, as our sole guide.

The resemblance of the forms just described to the trophosome of a calyptoblastic hydroid (sertularian or plumularian), after the disappearance of all the soft parts, is sufficiently obvious. And it is this resemblance between the fossil graptolite and the recent chitinous skeletons of the sertularian and plumularian hydroids which has induced modern palæontologists to refer the fossil to the order Hydroida, regarding the lateral offsets as hydrothecæ and the main tube as the chitinous perisarc of the hydrocaulus*.

We shall presently consider whether the exact points of contact between the graptolites and hydroids have been indicated in this comparison.

The fact which most obviously opposes itself to an accept-

* The sertularian affinities of the graptolites have been strongly insisted on by Hall, who has greatly advanced our knowledge of these fossils in his classical work, 'Graptolites of the Quebec Group,' which forms one of the memoirs of the Geological Survey of Canada. On the structure and principal modifications of graptolites, the works of Barrande ('Graptolites de Bohême') and of Geinitz ('Versteinerungen der Grauwacken. Die Graptolithen') should also be consulted. The sertularian affinities of graptolites have also been defended by Mr. W. Carruthers, of the Botanical Department, British Museum; and I know of no one who has worked out this question with so much care and completeness: see especially his "Revision of the British Graptolites" in the 'Geological Magazine,' vol. v. The hydroid relations of the graptolites are also maintained from the same point of view by Dr. Nicholson in various publications, in which he has largely contributed to our knowledge of these bodies, and more especially in his 'Monograph of the British Graptolitidæ,' part 1, just published.

I must here express my thanks to Mr. Carruthers for the liberal way in which he has placed at my disposal his large collection of graptolites, and for the aid which I have derived from his extensive acquaintance with the literature of the subject; and to Mr. Woodward, of the Palæontological Department, British Museum, for the readiness with which he placed in my hands for examination the fine collection of graptolites in the Museum.

ance of the hydroid affinities of graptolites is found in the presence of a virgula, the rod or "solid axis," which constitutes an essential feature in the structure of the graptolite. This rod was apparently of the same chitinous material as that which formed the rest of the firm skeleton of the graptolite. It is frequently continued for some distance beyond the distal or growing end, while its opposite or proximal end usually terminates in a minute spine ("radicle" of Hall), often continued into a long slender filament, like that of the distal end. It grows with the growth of the graptolite, as can be easily proved by following the progress of the graptolite from its younger stages; and it is difficult to explain its increase of length and thickness without regarding it, like the proper perisarc, as an excretion from the cœnosarc; and though, in the adult graptolite, it appears to have been separated by a chitinous film from immediate contact with the soft contents of the common tube, it was probably in direct relation with these in the younger stages, and would thus owe its existence to a special activity and peculiar modification of the chitine-excreting function of the cœnosarc at this part. It is sometimes found in the single-rowed graptolites to have become detached from the test or chitinous perisarc, leaving behind it a furrow in which it had lain, this furrow being, in the more perfect state of the fossil, converted into a tube by a thin extension over it of the test.

Though the virgula would thus form an extremely exceptional structure, its presence can hardly be regarded as offering an insurmountable obstacle to the admission of the graptolites into immediate relation with the Hydroida. Until lately a similar structure would have quite as justly excluded from the Polyzoa any animal which possessed it. The discovery, however, of the living polyzoal genus *Rhabdopleura* shows that a rod quite like that of the graptolite in all points, except in its not being continued beyond the cell-bearing portion, might be developed in an animal possessing in all other respects a typical polyzoal structure*.

It is true that the extension of the rod in the fossil beyond the limits of the common tube appears to increase the difficulty of reconciling its presence with the hydroid affinities of the graptolite. I believe, however, that this is, after all, not so anomalous a fact as at first sight it may appear, and that there is reason to believe that the cœnosarc invested by a proper perisarc was originally continued along what now ap-

* Allman, "On *Rhabdopleura*," in 'Quarterly Journal of Microscopic Science,' Jan. 1869, p. 57, pl. 8.

pears as a free extension of the rod. Its distal extension would then correspond to what had been the young growing portion of the graptolite, as yet destitute of denticles and with its perisarc so delicate as to be incapable of preservation in the fossil, so that the thin perisarc has perished along with the soft cœnosarc it included, its thicker rod-like portion being the only part preserved.

This view is borne out by the fact that in the very young stage of the graptolite a distal extension of the body along the rudimental rod, and beyond the incipient denticles, may be noticed; while it is further confirmed by an observation by Dr. Nicholson*, who tells us that in some specimens of *Diplograptus pristis* he has seen the common canal without denticles continued on each side of the prolonged rod.

The continuation of the rod beyond the denticle-bearing portion at the proximal end of the graptolite may also have been accompanied by an extension of the cœnosarc and its enveloping perisarc in this direction, the rod alone remaining in the fossil. To this view an observation of Mr. Carruthers† gives support; for he has noticed the prolongation of the rod at the proximal end of *Climacograptus scalaris* frequently invested for a short distance by a sheath.

If this explanation be accepted, the continuation of the rod as a naked filament beyond the denticle-bearing portion of the graptolite need no longer surprise us. A comparison of the rod with the chitinous spines which bristle over the surface of *Hydractinia* may also here suggest itself; but these spines are not only invested by a cœnosarcal layer, but are permeated by canals which are lined by cœnosarc, while in other respects the approximation of the graptolites to *Hydractinia* offers too many difficulties to allow of its being attempted.

The lateral spines often present at the proximal end of the graptolite seem to be of a different nature from that of the rod, and would rather appear to be referable to the same group of structures as the chitinous spines and variously formed processes by which the hydrothecæ and other parts of the perisarc of living hydroids are not unfrequently ornamented.

It has been already said that the advocates of the hydroid nature of graptolites regard their calicles or hollow lateral offsets as hydrothecæ. If this be really the nature of these parts, the mode in which their cavity opens into that of the main tube is exceptional; for in the living hydroids the point of communication between the hydrotheca and tube of the

* Geological Magazine, vol. iv. 1867, p. 261, note.

† In the 'Intellectual Observer' for June, 1867, p. 370.

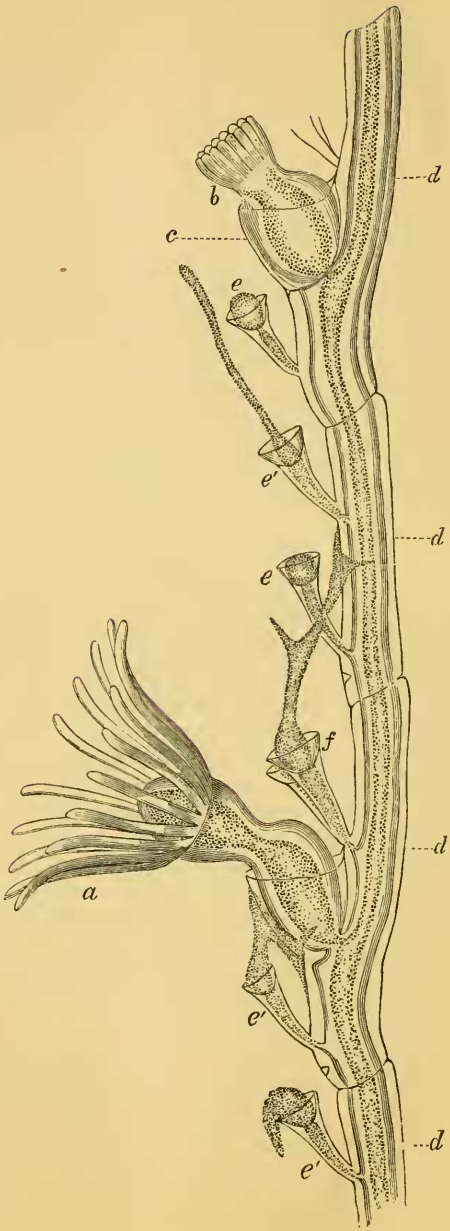
hydrocaulus is more or less constricted, or even provided with an imperfect diaphragm, so that the hydrothecæ become proper chambers, completely differentiated from the common perisarcal tube (figs. 2 & 3). Now the calicles of the graptolite have their cavity uninterruptedly continuous with that of the main tube, there being no diaphragm or constriction of any kind at the point where the one passes into the other (fig. 1)*.

There is, however, another view of the calicles which will meet this difficulty, a view suggested by the remarkable bodies known as nematophores, and which are characteristic of the Plumularidæ. These bodies constitute cup-like appendages formed of chitine and filled with protoplasm, which has the power of emitting pseudopodia or amœboid prolongations of its substance, and having their cavity in communication with that of the common tube of the hydrocaulus. They present two principal modifications, the movable and the fixed. In the movable forms (fig. 2) the nematophore always springs from a narrow point of attachment, whence it rapidly widens towards the distal end, while its cavity is divided transversely by an imperfect septum into two chambers. The nematophores of this form are more or less movable on the narrow point of attachment and are frequently caducous. They are characteristic of the genera *Plumularia* proper, *Antennularia*, &c. The fixed forms (fig. 3) commence with a wide basis of attachment by which they are immovably fixed to the hydrocaulus; and they are usually, though not always, destitute of an internal septum. They are never caducous. These are characteristic of such genera as *Aglaophenia*, where (as is also the case with the movable nematophores of other genera) they are situated, some upon the median line, when they are necessarily azygous, and some laterally, when they are in pairs. It is more directly with these fixed forms that I would compare the calicles of a graptolite; and such a comparison will show how exact is the resemblance. I have elsewhere shown that the tooth-like processes which project from the edges of the hollow leaflets which form the walls of the corbula in *Aglaophenia* (fig. 5, F, *c*) are bodies of an entirely similar kind; and the resemblance between these and the tooth-like processes of many graptolites is complete.

Now it is not alone in general form that the nematophores of *Aglaophenia* resemble the calicles of a graptolite. The mode in which their chitinous sheaths are seen to open into the common

* M'Coy ('Brit. Pal. Foss.') speaks of a septum at the base of the calicles in certain graptolites; but subsequent observations have not tended to confirm this statement.

Fig. 2.



Portion of a ramulus of *Antennularia antennina*, with hydranths and movable nematophores, showing the protoplasmic contents of the nematophores and the emission of pseudopodia.

a, hydranth extended; *b*, hydranth retracted; *c*, hydrotheca; *d*, *d*, *d*, consecutive segments of the ramulus; *e*, *e*, azygous or mesial nematophores with their protoplasmic contents quiescent; *e'*, *e'*, *e'*, azygous nematophores with their protoplasmic contents emitting pseudopodial prolongations; *f*, a pair of geminate or lateral nematophores, from one of which a thick branching pseudopodial process of protoplasm has been emitted.

canal of the perisarc (see fig. 3) after the destruction of all the soft parts is entirely similar to the mode of communication between the calicles and the common canal in the fossil (in those cases, at least, in which the graptolite has afforded facilities for examination such as to leave no doubt as to the structure of the parts in question), and quite different from that in which the proximal extremity of the hydrotheca is connected with the common tube of the chitinous perisarc in the existing hydroid*.

I cannot help believing that this is the true view to take of the morphology of graptolites. If so, the graptolites would admit of an approximation through an unexpected channel with the Plumularidæ. They would then be morphologically plumularians in which the development of hydrothecæ had been suppressed by the great development of the nematophores, probably the mesial ones†; while, on the other hand, the existing plumularian with well-developed hydrothecæ would present in its nematophores the last traces of the structure of its ancient representative, the graptolite.

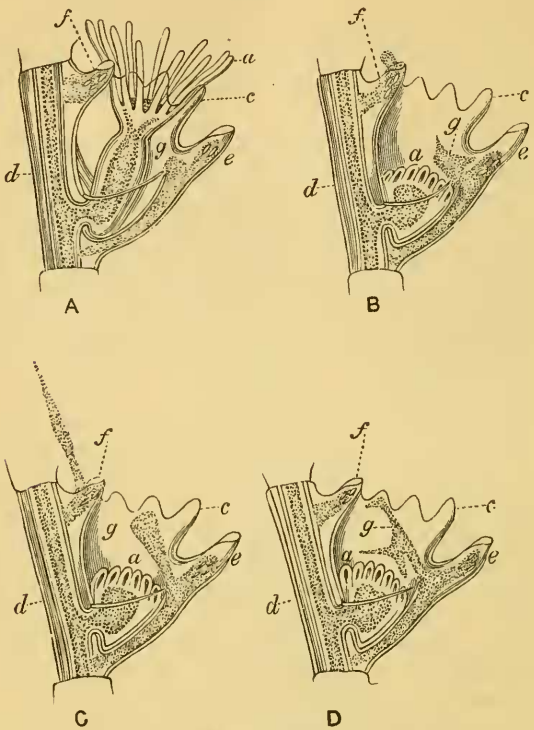
That the complete suppression of the hydrothecæ simultaneously with the retention of the nematophores is no overstrained supposition, will be admitted from what may be seen in certain plumularian hydroids which carry peculiar branches destined for the support of the gonangia or generative capsules. Now these branches are always destitute of hydrothecæ; but they are richly supplied with nematophores, which are distributed along the length of the branch, sometimes in a single row like the denticles of the monoprionidian graptolites, and sometimes in two opposite rows, like those of the diprionidian forms. In one undescribed species, from the deep-sea dredgings of the 'Porcupine,' I have found quite similar branches sent off from parts where they can have no connexion with the generative functions of the colony. The resemblance

* In the older parts of the hydroid stem the chitinous walls may become much thickened by successive layers of chitine, and the communication between the common canal and the cavity of the nematophore may thereby become contracted—a condition, however, which must not be confounded with the nature of the communication between the hydrotheca and its supporting stem.

† It may be here suggested that while the calicles of the monoprionidian graptolites have their representatives in the azygous or mesial nematophores of the plumularian, those of the diprionidian graptolites are represented by the paired or lateral nematophores. I should not hesitate to maintain this view, were it not that the comparison of a pair of opposite calicles in a diprionidian graptolite with a pair of lateral nematophores in a plumularian could hardly be reconciled with the view which would (apparently with reason) regard the diprionidian forms as morphologically representing two monoprionidian forms united back to back.

of these branches with their rows of nematophores to certain graptolites with their rows of calicles is too obvious to be overlooked.

Fig. 3.



Hydrothecæ of *Aglaophenia pluma*, with hydranths and fixed nematophores.

A. Hydrotheca with the hydranth extended and with the protoplasmic contents of the nematophores quiescent: *a*, hydranth; *c*, serrated margin of hydrotheca; *d*, segment of the ramulus, carrying the hydrotheca; *e*, mesial or azygous nematophore; *f*, lateral nematophore; *g*, lateral aperture through which the cavity of the nematophore communicates with that of the hydrotheca.

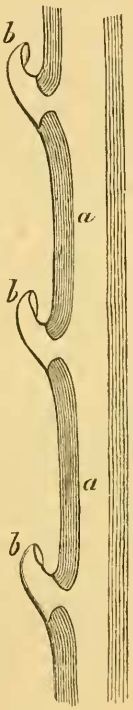
B. Hydrotheca with retracted hydranth and with the protoplasmic contents of the nematophores emitting pseudopodial prolongations: *a*, hydranth; *c*, margin of hydrotheca; *d*, segment of the ramulus carrying the hydrotheca; *e*, mesial nematophore with its protoplasm projected in an irregular pseudopodial mass, *g*, through its lateral aperture into the cavity of the hydrotheca; *f*, lateral nematophore with the commencement of a pseudopodium.

C. Same parts, with pseudopodial processes more advanced.

D. Same parts, showing different states of extension of the pseudopodia.

To the views here maintained further support is given by certain undescribed hydroids in the collections of the United-States Coast Survey placed in my hands for determination. Among these are some plumularians in which that part of the stem which lies at the proximal side of the pinna-bearing portion (and is accordingly destitute of hydrothecæ) carries along its length a single row of fixed nematophores separated from one another by regular intervals, and appearing to take the place of hydrothecæ (fig. 4). This part of the hydroid, if detached from the pinnate portion, might (except from the much greater slenderness of both common tube and calicles in the fossil than in the living form) almost be taken for a recent *Rastrites*.

Fig. 4.



Portion of the stem from the proximal side of the pinnæ in an undescribed plumularian from the Gulf-stream, showing the distribution of nematophores along its length.

a a, part of the common canal, with the walls thickened by successive layers of chitine; *b, b, b*, nematophores.

Still further, the very important aid afforded in such questions as the present by the history of development may be here adduced; for in the plumularian genus *Antennularia* the embryonic stem is provided with well-developed nematophores before any hydrothecæ have made their appearance.

Whether the calicles of the graptolites gave lodgment to true hydranths, or were filled with simple protoplasm, as I have already shown to be the case with the nematophores of the living Plumularidæ, it is, of course, impossible to assert with confidence. If, however, we give analogy its full weight, and extend the resemblance between the calicles of the graptolites and the nematophores of the plumularians to the nature of their contents, we should then have lodged in the graptolite-calicles, not hydranths, but simple masses of protoplasm, capable of emitting pseudopodial prolongations, on which would devolve the duties of conveying nutriment to the colony. The graptolites would thus not merely manifest relations to

the Hydroida, but would exhibit others at least as strong to the Rhizopoda. Indeed but a step would be needed to convert such an organism into a true rhizopod; for if the common canal as well as the calicles were occupied by protoplasm, the whole might then be compared to an association of such rhizopodal forms as *Gromia*, united into a composite colony by a common tube filled with a common mass of protoplasm.

A very general feature in the mode of growth of graptolites is found in the fact that while the entire graptolite continues to increase in length, the denticles which are situated towards the proximal end remain of smaller size than those which succeed them, while, after thus increasing in size towards the middle, they again often diminish towards the distal end, the broadest part of the graptolite being consequently in this case near the middle. It may also be noticed that the denticles towards the base of the graptolite occasionally differ from those which succeed them, not only in size but in form.

Now, setting aside the undeveloped condition of the hydrothecæ near the growing or distal point of the stem, I know of nothing like this among the living Hydroida; while, on the other hand, the nematophores of the Hydroida vary in form in one and the same colony, and are sometimes found more or less arrested or otherwise modified towards the proximal end of the branch.

In support of the hydroid nature of graptolites, the occurrence of generative capsules in these fossils has been recently adduced; and as this is a matter of great importance in the present question, we shall here consider the evidence on which it rests.

Hall has described and figured in one of the double-rowed graptolites (*Diplograptus*) certain appendages of an irregularly triangular shape, having one angle continued into a narrow band, by which they become attached to the body of the graptolite. They are arranged with considerable regularity in two opposite rows, which extend for some length along the sides of the graptolite. These appendages are compared by Hall to the gonangia of a calyptoblastic hydroid*.

I am indebted to Mr. Etheridge for an opportunity of examining a British specimen of a *Diplograptus* which carries bodies of undoubtedly the same nature as those of Hall, and to Mr. J. Hopkinson, who had previously examined this specimen and determined its nature, for the inspection of an excellent enlarged drawing of it, which has since formed the subject of

* Hall, 'Graptolites of the Quebec Group,' p. 32, pl. B. figs. 6–11.

a woodcut accompanying Mr. Hopkinson's description of the specimen lately published in the present Journal*. Now, after a full consideration of Hall's and Hopkinson's descriptions and a careful examination of Mr. Etheridge's specimen, while I admit the probability of the appendages in question belonging to the generative system, I am unable to satisfy myself that they are the remains of gonangia. Indeed they do not appear to me to be capsular bodies at all, but rather double laminæ, though the way in which they are occasionally folded over on themselves, as seen in Mr. Etheridge's specimen, may give them the deceptive appearance of having been capsules, while in reality this condition would be inconsistent with their alleged capsular form.

The regularity of their disposition, and the close resemblance between those of the American specimens and those of the British, will not allow us to regard them as mere parasitical or accidental growths; and I believe that their connexion with the generative system of the graptolite may be considered probable. If so, then it remains for us to determine the parts which represent them in the living hydroid; and these I believe will be found in the leaflets which compose the corbulæ, or basket-shaped receptacles of the generative capsules, in *Aglaophenia* (fig. 5).

The two rows, then, of appendages in the graptolite would, according to this view, represent a corbula; and the gonangia or generative capsules, if such had existed, would have been borne upon the front of the graptolite along the bases of the appendages. We should hardly, however, expect to find any remains of gonangia in the fossil; for in all living hydroids which have their gonangia protected by corbulæ these gonangia are as delicate and perishable as the naked generative sacs in the *Gymnoblastea*.

The corbulæ of the graptolites, if such really had existed, were probably open ones, like those of the living *Aglaophenia myriophyllum*, and of several species from extra-European seas—a condition which indicates a low stage of differentiation, and represents a form through which the closed corbula of *Aglaophenia pluma* &c. passes in the course of its development (fig. 5, A, B, C, & D).

The view here adopted of the nature of these supposed generative capsules in the graptolite receives support from the fact that in every case where they have been satisfactorily observed the denticles of the graptolite become suppressed

* See 'Ann. Nat. Hist.' for May 1871.

in that part of the fossil which carries the appendages*, a fact quite in accordance with what we know of the corbulæ in the living hydroids; for in these the hydrothecæ with their accompanying nematophores are replaced by the leaflets of the corbula, while the naked gonangia of other hydroids are never accompanied by an atrophy or other alteration of the hydrothecæ or neighbouring parts.

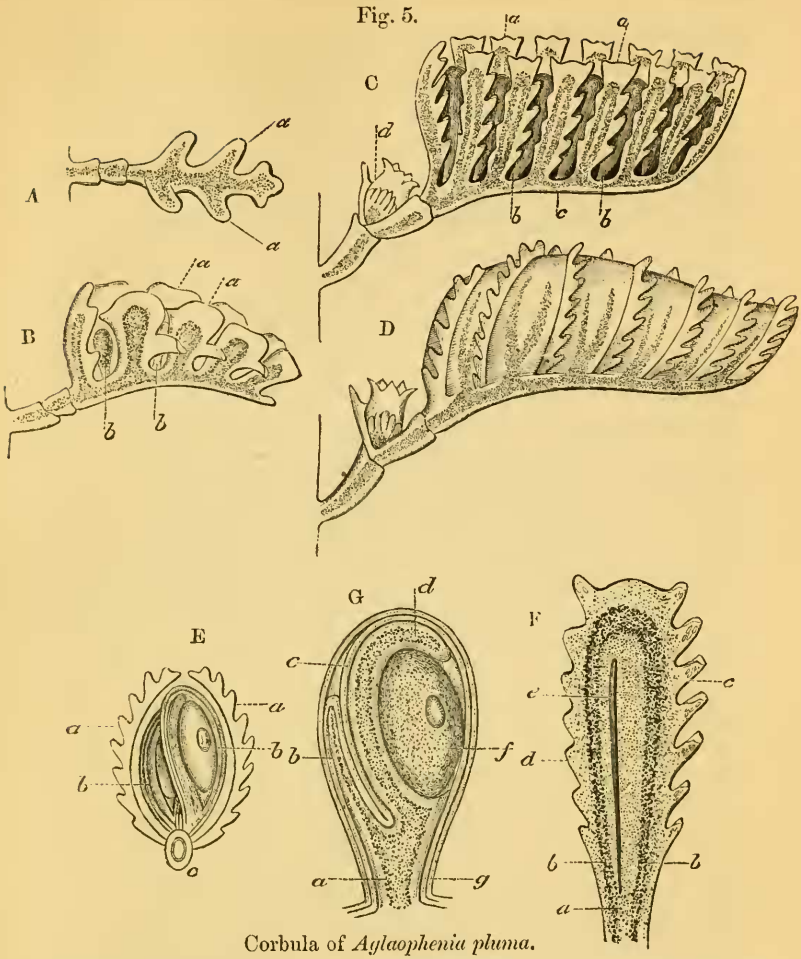
In both the American and British specimens the appendages in question seem to have been supported by a framework of branched chitinous filaments which remain behind after the destruction of the intervening membrane. The existence of these filaments probably depends on the same morphological conditions as those which determine the presence of the chitinous axial rod; and it must be admitted that we have no known analogy for them in any living hydroid, unless the internal narrow chitinous lamina which passes like a midrib through the corbula-leaflet (fig. 5, F, *e*) admits of being compared with them.

This comparison of the appendages of Hall to the corbula-leaflets of an *Aglaophenia* is in harmony with the view here advocated as to the nature of the calicles of the graptolite, which we have compared to the nematophores of an *Aglaophenia*. I believe the corbulæ of the living *Aglaopheniæ* to consist essentially of a special and excessive development of the nematophores; so that the graptolite, not only in its trophosome, but also in its gonosome, would thus present us with an instance of the great development of the nematophoral system at the expense of the hydranthal.

This view of the morphology of the corbulæ, in some cases at least, seems placed beyond doubt by their formation in an undescribed *Aglaophenia* from the deep-sea dredgings of the United-States Coast Survey. The leaflets which form the walls of the large and beautiful open corbulæ of this hydroid are mainly composed of the greatly enlarged and transformed nematophores which in the unaltered ramulus lie in front of the hydrothecæ. The hydrothecæ of the parts which become transformed into cor-

* Hall notices a case (*loc. cit.* p. 33, pl. B. fig. 9) which he regards as one in which the appendages are present in a graptolite which still retains its denticles. This, however, is by no means a well-marked instance, and one might be permitted to doubt the identity of the structures here figured with the appendages previously described by him. In Mr. Hopkinson's woodcut also, the denticles are represented as well developed for some distance on that part of the graptolite which carries the appendages; I cannot satisfy myself as to the reality of this in the actual specimen; indeed the woodcut does not do justice to the excellent original drawing kindly sent to me for inspection by Mr. Hopkinson.

Fig. 5.



Corbula of *Aglaophenia pluma.*

A. Very young corbula; B. Corbula more advanced; C. Corbula in a still more advanced stage; D. The mature corbula; E. Transverse section of mature corbula, showing two of its contained gonangia, each with a single gonophore: *a*, *a*, leaflets of corbula; *b*, *b*, gonangia; *c*, ramulus which supports the leaflets; *d*, a hydrotheca.

F. Separate leaflet from mature corbula: *a*, continuation of the cavity of the supporting ramulus into the leaflet, where it divides into two branches, *b*, *b*; *c*, nematophores, forming tooth-like processes on the distal edge of the leaflet; *d*, imperfectly developed tooth-like processes on the proximal edge; *e*, imperfect septum partially dividing the cavity of the leaflet.

G. Gonangium from mature corbula: *a*, continuation of somatic cavity into gonangium; *b*, blastostyle partially suppressed by the enlarging gonophore; *c*, gonophore; *d*, spadix; *f*, ovum; *g*, chitinous wall of gonangium.

bulæ are not here actually suppressed, but remain of somewhat smaller size, affording the clue to the morphology of the entire organ; and it can be plainly seen that it is the mesial nematophore of each of these arrested hydrothecæ which has become enormously developed and flattened out so as to form the leaflet of the corbula-walls, while at the same time it becomes complicated by carrying along one edge a row of small tooth-like nematophores, as in the corbula-leaflet of *Aglaophenia pluma* &c. The hydrothecæ, with their nematophores, which in the untransformed ramulus constitute a single series along the front of the ramulus, are, in order to form the walls of the corbula, thrown alternately from side to side.

If these views be accepted, we shall have nearly the entire graptolite in those instances in which the appendages of Hall have been noticed converted into a corbula, a state of things which naturally follows from the simple unbranched form of the fossil. The graptolite has, in fact, become greatly changed in form, and modified for a special reproductive function in a way which reminds us of the so-called fertile fronds of certain ferns as distinguished from the so-called sterile fronds.

It is true that the great rarity of these peculiarly modified graptolites is opposed to what we know of living hydroids; for among these we are not acquainted with a single trophosome which we are not justified in believing destined at some period of its life to develope a gonosome. A case, however, bearing some analogy to that of the graptolites would be afforded by fossil ferns; for we know how rare a thing it is to find, among the vast multitudes of individuals with which the coal-measures abound, specimens bearing fructification.

While the graptolites would thus seem to contrast with living hydroids in their rarely developing a gonosome, it is interesting to see them contrasting also in another respect—namely, in their free if not floating habit. And here we are reminded of the gulf-weed of the Sargasso sea; for, throughout the thousands of square miles over which the floating meadows of this remarkable plant extend, no one has yet succeeded in finding a single specimen in fructification, though the fructification of closely allied species, which grow attached to rocks like ordinary seaweeds and like the rooted trophosomes of the hydroids, is well known.

Certain bodies found associated with graptolites in the Silurian shales of Dumfriesshire have been described by Dr. Nicholson, who regards them as the "ovarian vesicles" of the graptolites, and as proving the hydroid nature of these fossils*.

* Nicholson, in 'Geological Magazine,' vol. iv. 1867, p. 259, pl. 2.

He describes them as "oval, bell-shaped, pyriform, or rounded, provided with a mucro at one extremity, and surrounded entirely by a filiform border, resembling in texture the axis of a graptolite." They attain a length of nearly half an inch.

He has found them not only free, but in many cases attached to the graptolite, not, however, to any constant point; for some spring "from the common canal, others from the apex of a cellule, and others from the under surface of a cellule, the last two modes being the most frequent."

The largest of these capsules which he has seen attached did not measure more than a tenth of an inch in diameter; and Dr. Nicholson believes that at this stage they become detached, and then attain the large size he has observed in the specimens found free in the shale; for he has there found them in all stages of growth, from small rounded bodies, not larger than a pin's head, to bodies nearly half an inch in length.

Whatever these bodies may be, it is plain that Dr. Nicholson's account of them is irreconcilable with the supposition that they represent either the gonangia or the gonophores of a hydroid; for, apart from their supposed development after detachment from the colony, their origin from the walls of the denticle is alone decisive on this point. Indeed their connexion with the graptolite appears to be purely accidental.

Hall has called attention to the occurrence, in the same beds which contain the graptolites, of minute free bodies which he regards as the young or "germs" of the graptolites*. In their earliest form they would appear to consist of a little chitinous oblong sac traversed longitudinally by a slender chitinous filament, which is continued for a little way at both ends beyond the sac, while at one end it is accompanied by two minute lateral spine-like processes.

This early form has been traced through more advanced stages, in which it has been seen to become more and more elongated, to develope denticles along its length, and finally to attain a form in all essential points identical with that of an adult graptolite.

Others, slightly differing in shape from those described by Hall, have been also obtained. Indeed these young graptolites (for there is little doubt that Hall is right in so regarding them) are now well known. They are by no means uncommon in graptolitic shales, in some examples of which I have seen them abounding in countless multitudes.

Hall believes that he finds evidence of their having been contained within the so-called reproductive vesicles of the

* Hall, *op. cit.* p. 33, pl. B. figs. 12–19.

graptolite. From his account of their relation to these, however, I can recognize nothing but accidental proximity; while if we admit that he has grounds for this belief, we should then have, in the advancement of the embryo to a stage in which it has become covered by a chitinous perisarc previously to liberation, a state of things quite at variance with all we know of the reproductive phenomena of living hydroids.

It is not improbable, however, that these graptolite "germs" of Hall are free zooids rather than true embryos, and that they had been originally thrown off by a process of non-sexual reproduction from some part of the living graptolite in a manner which reminds us of somewhat analogous bodies which I have elsewhere described as becoming detached from true hydroids in the case of *Schizocladium* and of *Corymorpha*. As we descend through the great biological groups it is no uncommon thing to find the faculty of agamic reproduction becoming intensified, until in the lowest members of the group we see it (as in the case of the gulf-weed already referred to) taking more or less the place of true sexual generation.

But little requires to be said regarding other views which have been from time to time advanced as to the affinities of graptolites.

Their alleged polyzoal affinities, however, have some claim on our acceptance. Indeed, were it not for the discovery of the probable graptolite gonosome (corbulæ?), we should have nearly as much to say for this view as for that which would refer them to the Hydroida, more especially as the discovery of *Rhabdopleura* renders us acquainted with a polyzoon in whose test is developed a chitinous rod in almost all respects like that of the graptolites*.

On the whole, then, it would seem that the graptolites constitute a very aberrant hydrozoal group having manifest affinity with the Hydroida, to which they are connected by the nematophore-bearing genera of the latter, while they have also important points of connexion with the Rhizopoda. The undoubted members of this group are further characterized in an eminent way by the possession of a solid supporting rod; and it is this feature which has suggested to me the name of RHABDOPHORA, by which I have proposed to designate them.

* The comparison of the rod of *Rhabdopleura* with that of a graptolite has already been made by Dr. Nicholson ('Manual of Zoology'), though he adopts the more generally accepted view which finds hydrozoal rather than polyzoal affinities in the graptolites.